BREEDING BEHAVIOR OF THE MERLIN: THE COURTSHIP PERIOD

JOHN W. FELDSINE AND LYNN W. OLIPHANT

ABSTRACT - Behavioral observations were made on an urban population of the Merlin (Falco columbarius richardsonii) nesting in the city of Saskatoon, Saskatchewan. Fourteen distinct behavioral displays and four vocalizations were identified during the courtship period. The behavior of the birds was remarkably similar in most respects to large falcons such as the Peregrine Falcon (F. peregrinus), Prairie Falcon (F. mexicanus) and Gyrfalcon (F. rusticolus), which have been studied more thoroughly.

Information on the breeding behavior of the Merlin is scanty and sometimes contradictory. Brown (1976), referring to the British Merlin (F.c. aesalon), states that "Merlins do not perform spectacular aerial display flights" while Cramp and Simmons (1980) briefly mention such aerial displays. Most of the literature dealing with Merlin breeding behavior focuses on the nesting and raising of young (Rowan 1921-22; Craighead and Craighead 1940; Lawrence 1949; Campbell and Nelson 1975) with little information on behavior during the courtship period. This study was designed to compile an ethogram of the behavior of the Merlin from pair formation to the time of egg laying.

Methods

Most of the observations were made on a population of Merlins nesting in Saskatoon, Saskatchewan, a city of 1220 ha. and a population of 155,000 (see Oliphant 1974 and Oliphant and Haug 1984 for details of this Merlin population). Data were obtained during a behavioral study conducted in 1982 and 1983 by John Feldsine supplemented by casual observations between 1971 and 1984 by Lynn Oliphant (estimated 800 h). During the 2 yr study 16 nest sites were visited each year from mid-January to the end of April. A tape recording of Merlin vocalizations was played at each site to draw out concealed birds and to initiate behavioral displays. Scattered observations were made at several nest sites throughout the day but the majority of observations was made between sunrise and 1100 H. In addition, intensive observations of 2 pairs of Merlins were made in 1982. A total of 175 h of observations were made on these birds between February 17 and April 30 from a parked vehicle using binoculars and a spotting scope between sunrise and 1400 H. Casual observations were also made In 1982 on a pair of Merlins that raised young in captivity.

RESULTS

We were able to recognize 14 courtship displays and 4 primary vocalizations. The displays are in some cases comprised of several components, which may be employed in more than one display. Not all of the displays described were seen in both of the intensively studied pairs. These 2 pairs represented the seasonal extremes in terms of appearance on territory; 1 pair was first observed courting on territory on 16 February, the other not until 14

April. The early pair was not as elaborate or expressive in its displays as was the late arriving pair, nor did it display so frequently.

Vocalizations

- 1. Ki-ki-kee (Kek-kek-kek). This is the most commonly heard call and takes on several different forms, which vary in intensity, speed, rhythm and number of syllables according to the situation. It is used by both sexes with the male's call higher in pitch and more rapidly delivered. This call accompanies several courtship displays and territorial or other aggressive encounters, although in an aggressive context, it is deeper and resembles a kac-kac-kac sound (Craighead and Craighead 1940).
- 2. Tic (Chip). Used by both sexes in almost all courtship rituals and is typically repeated several times at intervals of a few seconds. Again, the male's call is higher in pitch than the female's. Often this call is given alternately by the pair, especially when near each other but not in visual contact.
- 3. Copulation Chutter (Copulation Bleat, Chrrr). Somewhat like the sound made by a short blast on a police whistle. When used by the male, this call indicates a desire to copulate. Females occasionally use it in encounters involving food, e.g., when the male returns with prey but fails to signal for a food transfer. This may indicate an extremely hungry female. Also used by non-resident birds of either sex when approaching a resident female.
- **4. Food Begging Whine.** Used strictly by the female and consists of a series of monotonous whining notes resembling a very slow ki-ki-kee. It apparently tells the male either "give me the food that you have" or "go get me some food". Occasionally females gave this call before, during and after a copulation sequence. It resembles and is presumably derived from the begging call of the young.

Courtship Displays

1. Power Flying. One of the earliest male courtship displays and may continue throughout

the courtship period. It consists of a strong flapping flight with deep wingbeats accompanied by rolls which alternately display the dorsal and ventral aspects of the plumage when viewed from the side (Fig. 1.1). Power Flying may be terminated by a Slow Landing Display, Power Dive or a Rocking Glide usually past a perched female and/or potential nest tree. Power Flying is used as a territorial display to a rival or potential or existing mate. When performed in the presence of a rival male it reaches its greatest intensity. We have observed 2 males from adjoining territories Power Flying past each other at their common boundary. The Tic-Tic vocalization is usually given during this display. Volume and frequency of the vocalization and snappiness of the rolling vary with the intensity of the display. One male was observed Power Flying repeatedly over a period of about 1 wk following the death of his mate just prior to egg laying. No other birds were observed in the area during these displays suggesting that Power Flying may be used to attract potential mates into a male's territory.

- 2. Power Diving. Another male display which appears to be a more intense variation of Power Flying with the only major difference being the angle of flight (Fig. 1.2). This display may be initiated by a direct high-level climb over the territory or preceded by Power Flying at heights which may reach several hundred meters. The steepness of the dive may vary from about 45° to near vertical. Flapping flight may continue throughout the dive accompanied by 180° rolls. As speed increases the wings are partially folded. The dive may be terminated with a U-shaped climb or often by Power Flying or a Rocking Glide display past a potential mate or nest site. The context of this display is one of territory defense and advertisement. This display was most often precipitated by one or more rival males on the resident male's territory. As many as 4 birds were present on some occasions, and we suspect that the female copulated with one of the rivals as well as the resident male. Cramp and Simmons (1980) report that pairs were observed Power Diving together. We have never observed females Power Flying or Power Diving.
- **3. Rocking Glide.** A less intense version of Power Flying (Fig. 1.3). The components of the 2 displays are similar except that there is no flapping flight with the Rocking Glide. The falcon initially flaps to build up speed or comes out of a Power Dive and then sets the wings to glide. It then performs

90° - 180° rolls depending upon the speed attained beforehand. As in the previous 2 displays the rolling component of this display alternately flashes the blue back and contrasting lighter underparts of the male. The plumage contrasts are not so obvious when the display is performed by females or immatures. Probably as a result of the slower flight speed, the tail and wing feathers are somewhat more flared than when Power Flying.

This is a fairly common display and was frequently indulged in by both sexes, although more often by males. Males may use this display to attract mates to their territories or upon return to an established territory. In the latter situation the male begins rocking and sounding the Tic-Tic call when passing by a perched female. The use of this display by females was more aggressive and was most often observed in response to a taped female call. Females are often more aggressive than males in defense of the nest site, and intruding females often elicited a Rocking Glide display from a resident female. This display was often terminated with a Slow Landing display at the nest tree.

- **4. Flutter Flying.** A common aerial display and may be observed almost daily at an active nest site. The flight pattern is usually circular or figure-eight shaped (Fig. 1.4). Flight speed is slow with rapid shallow wing beats generally below the level of the body. It is similar to the fluttering flight of the Eastern Kingbird (*Tyrannus tyrannus*). The flight often terminates in a Slow Landing display. Flutter Flying probably functions as a mild territorial advertisement and/or display to a perched mate. The Ki-ki-kee and/or Tic-Tic vocalizations are usually given by the flying male, and the female often answers.
- **5.** High Circling/Soaring. Although the Merlin is often reported as never soaring, we often observed 1 or more (up to 4) birds circling at heights up to several hundred meters. These birds often set their wings and soared if conditions were favorable. Circling/Soaring was seen by both resident and non-resident birds of both sexes. In the former it probably served as a mild territorial display while for the latter it may serve as a means for surveying another territory from an advantageous position.
- 6. Slow Landing Display (Hitched Wing). Commonly a terminal component of other displays, the Slow Landing display is a male display made while coming in to perch (Fig. 1.5). The flight pattern when approaching the perch is similar to

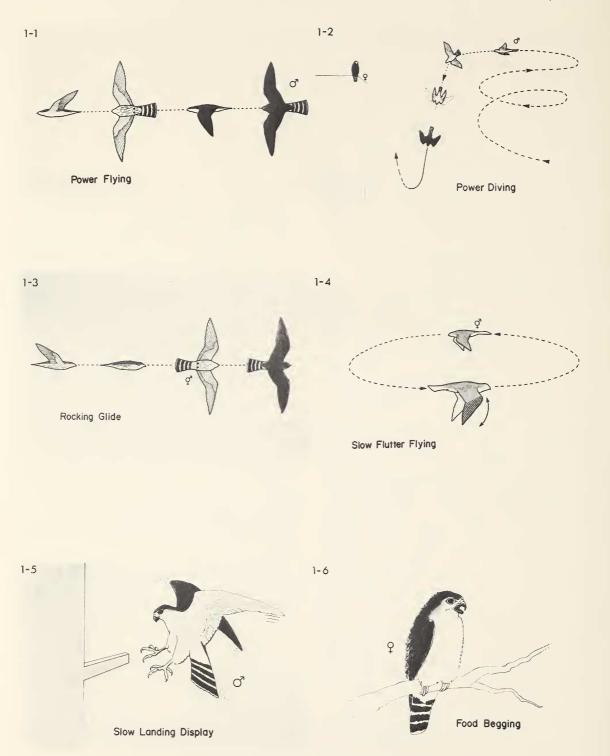
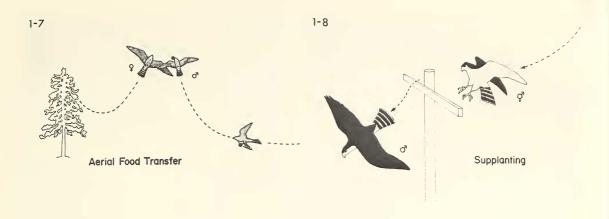
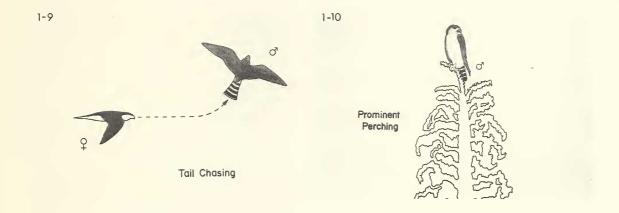
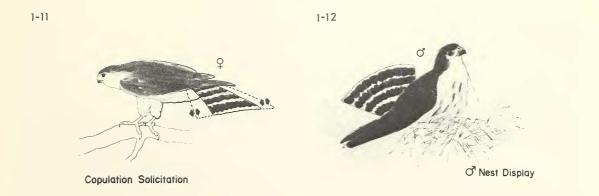


Figure 1. Diagramatic representations of twelve major courtship displays of the Merlin. Symbols (\mathfrak{F}) indicate the sex of the bird typically making the display.







(Continuation of Figure 1.)

the flight when approaching for copulation. The body attitude varies from about 45° to nearly vertical and the legs are dropped. Movement is almost entirely confined to the outer wing, and the tail is generally fanned. Forward progress is slow and owl-like. The bird alights stiff legged with head bowed. Slow Landing may occur immediately before or after copulation and may also be a terminal component of other aerial displays. When used before copulation, the copulation chutter may immediately precede the Slow Landing display. On other occasions the Ki-ki-kee call is given during the flight or no vocalization is given.

7. Food Begging. A female display generally made from a perch. When perched, the bird sits with puffed out plumage (Fig. 1.6) and emits a series of monotonous whines or wails, very much like a slow Ki-ki-kee. Intensity and duration of the call is probably a good indication of hunger level. If very hungry she may flit from perch to perch emitting the wails constantly. Often the male responds by initiating a food transfer. If he is without food, he may leave the territory, presumably to hunt. If he does not respond and has food, she may fly to him and initiate a Forced Food Transfer by snatching the prey from him. If he is without food she may supplant him from his perch. When supplanted, the males usually left the territory presumably to hunt. The begging call is given almost constantly during all of these actions and sometimes continues after the male has disappeared. This display is performed exclusively by the female and is very similar to the begging behavior of nestlings. It reaches its maximum intensity a few weeks prior to egg laving.

8. Food Transfers. We have observed 3 forms of this display: air-to-air, perched, and air-toperch. Air to air transfers occur with the female flying out to meet the male as he returns to the nest site with food (Fig. 1.7). The birds fly toward one another and rise in a simultaneous, nearly vertical stalling climb until they are nearly breast to breast. The male will often have transferred the food to his beak. As they pass closely in the air the female reaches out with a foot and grabs the prey. Rowan (1921-2) calls this behavior Courtship Feeding and considers it to occur only rarely. Aerial transfers are much more common after the young have hatched than during courtship period. Perched food transfers take place much as described by Wrege and Cade (1977) for the Peregrine (Falco peregrinis) with bowing and sounding of the Ki-ki-kee and/or Tic calls by both birds. The female sometimes makes the Food Begging whine during the entire ritual. On occasion the females seemed irritated, aggressive and probably hungry. They flew quickly to the male's perch, often running towards him upon landing, grabbed the food without display or ceremony (a Forced Food Transfer). A variety of calls was heard during these encounters, a very excited and aggressive sounding Ki-ki-kee, a Copulation Chutter, or the Food Begging whine from the female, and a rapid, high pitched Ki-kikee from the male. During Air to Perch Transfers either bird may remain perched. If the male perches he transfers the prey from foot to beak and the female flies by and grabs it with a foot. Food transfers begin rather late in courtship and increase in frequency towards the time of egg laying.

Food caching is common throughout the breeding cycle and is performed by both sexes (Oliphant and Thompson 1976). Ritualized caching of prey by the male within sight of the female followed by retrieval by the female is commonly observed in captive peregrines. Although we did not observe this in the Merlin, it may well occur.

9. Supplanting. During supplantations, 1 bird flies to another perched individual (generally a male) and drives that bird from its perch (Fig. 1.8). This behavior occurred in 3 different contexts: (1) a resident male supplanting a rival male, (2) the resident female supplanting her mate and (3) one or both resident birds supplanting an intruder such as an American Crow (Corvus brachyrhynchos) or Blacked-billed Magpie (Pica pica). An aggressive Ki-ki-kee call was usually heard during these encounters

In all contexts this behavior may be interpreted as a display of aggression and when used against intruders or rivals it also appears to be a defense of territory. When occurring between the mated pair, expression of female dominance seems the likely motivation and may be used to encourage the male to begin hunting.

10. Tail Chasing (Fig. 1.9). This behavior was only observed on a few occasions. Once a female was observed vigorously chasing her mate who had just returned with prey. While chasing him she repeatedly called using the Copulation Chutter. He eventually dropped the prey. At another location a female was observed chasing a male at great speed. He appeared and sounded as if his life was in grave

danger. The chase coursed around trees and shrubs 2 or 3 m off the ground. The pair soon disappeared and the outcome was not determined. Cramp and Simmons (1980) report that tail chases often end in copulation. Captive female Merlins have been observed to pursue actively their mates. These tend to be very aggressive interactions, and when this occurs in confinement, the male is sometimes killed (Campbell and Nelson 1974). The female from our captive pair caught and grappled with her mate on several occasions in 1982 just prior to egg laying. Clipping her primaries reduced her flight ability and normal mating occurred soon after. In 1983 this female killed the male in spite of having her primaries clipped. Apparently it is necessary for the male to have plenty of space in order to avoid being caught by the female.

11. Prominent Perching. Merlins often perch on a high vantage point near the nest site for long periods of time (Fig. 1.10). This is probably a territorial advertisement, but often appears to be simply loafing. The bird surveys the surrounding area constantly and occasionally may preen or sound the Ki-ki-kee or Tic-Tic calls. This was a commonly observed behavior most often involving the male, but occasionally the female. A large high rise building was often used by both sexes and acted as a focal point for many aerial displays by the males. Television antennas and certain trees (spruce and weeping birch particularly) also offered favored perch sites in Saskatoon.

12. Male Precopulation Display. The male has a number of ways in which he signifies readiness to copulate. He most often perches in a tree close to the tree where the female is perched and may call frequently (Ki-ki-kee and/or Tics). He may also bow and fan his tail. Just prior to flying to the female he stands tall, stares intently at the female and utters the Copulation Chutter one or more times perhaps in response to a mild solicitation by the female or perhaps attempting to initiate solicitation. When flying towards the female he uses the Flutter Flight with his legs dangling, often continuing to give the Copulation Chutter. Copulation ensues if the female is receptive with the final mounting of the male being similar to the Slow Landing Display.

13. Female Copulation Solicitation (Fig. 1.11). The female signals readiness to copulate by bowing deeply and fanning her tail. This often follows an exchange of vocalizations with the male and Precopulation Displays by the male. Both birds

typically vocalize during copulation. The female makes a modified hoarse Ki-ki-kee call and often makes a slow drawn out Ki-ki-kee immediatly following copulation while the male Chutters. The male often makes a Slow Landing Display following copulation. Copulation may occur very early during courtship (up to 3 or more months prior to egg laying) but becomes much more frequent (up to several times an hour) as egg laying approaches.

We have not considered copulation as a courtship display in itself, but it is obvious that copulations that precede egg laying by several weeks to months do not function in fertilization but rather to cement the pair bond.

14. Male Nest Display (Fig. 1.12). Both sexes enter potential nests and often make Tic vocalizations during the courtship period. Since it was generally impossible to observe the birds when on the nest, our only observations of this display (3) are from our captive pair which were watched from behind one-way glass looking into the nest. In this display the male lowered himself on the nest as if he were settling on eggs. He then extended his wings and drooped them and fanned his tail nearly vertical. He extended his head forward and then withdrew it while arching his back. The drooping wings were trembled throughout the display. As the head was extended forward, the tail and lower back were raised above the horizontal so as to display the fanned tail and dorsal plumage. The female was a passive observer on the edge of the nest during the entire display with the male facing the female. No vocalizations were given. This display is very similar to that of a juvenile House Sparrow (Passer domesticus) begging food from an adult, and was first reported by Fyfe (in Trimble, 1975).

Discussion

In describing the behavior of the Merlin, we have drawn somewhat arbitrary lines between individual displays or vocalizations as well as between what we classified as a complete display and what was simply a display component. Many behavioral actions (rocking in flight, bowing, tail flashing) were thus considered components of displays rather than displays in themselves. We have attempted to follow accepted terminology and classification from previous descriptions of falcon behavior although some deviation was necessary. For example, Wrege and Cade (1977) and Nelson (1977) consider the Head Low Bow to be a major display of the pereg-

rine. We do not consider it well developed enough in the Merlin to be considered any more than a component of other displays.

The difficulties of assigning a particular functional significance to displays that are probably often, if not always, multifunctional should also be recognized. The primary functions of behavioral displays during the courtship period include the establishment and defense of a nesting territory, attraction of a suitable mate and the establishment of a strong pair bond, all of which are necessary for successful breeding. Determining which of these functions are the primary focus of a given display is difficult to ascertain simply from the context of the situation without experimental manipulation.

Vocalizations

The courtship vocalizations used by Merlins are similar both in structure and context to those of the large falcons with which we are familiar (the Peregrine, Gyrfalcon and Prairie Falcon). They differ mainly in having a higher pitch associated with their smaller body size. The Tic call is the most divergent and is a short stacatto version of the large falcons' "Eechip" call. It is the most like the shortened "Chup" version of this call not having the high pitched initial segment. The Female Begging call or "Treble Whine" (Nelson 1977) and Copulation Chutter are almost identical to those of the large falcons, and the Ki-ki-kee is the equivalent of the large falcons' deeper Kac-kac-kac. In general, the Merlin is more vocal than large falcons with the possible exception of the Gyrfalcon which appears to have a more varied and frequently used vocal repertoire.

Courtship Displays

The courtship behavior of the Merlin and especially aerial displays has been largely overlooked in the literature (Rowan 1921-22; Trimble 1975; Cramp and Simmons 1980). In contrast to the conclusion of Cramp and Simmons that display flights are "rather inconspicuous and rarely observed," the Merlins we observed regularly performed complex aerial courtship flights that were nothing short of awesome. The Power Flying and Power Diving flights with side to side rolls are essentially identical to those described for the peregrine by Nelson (1977) and are presumably similar to other large falcons (Cade 1982). The impression given by the Merlin, while performing these displays, is one of a

much larger, heavier and more powerful falcon.

Other behavioral displays that the Merlin shares in detail with the peregrine include the Slow Landing Display, High Circling/Soaring, Prominent Perching, Flutter Flying, Female Begging, Food Transfers and Supplanting. Bowing is much less prominent in the Merlin than large falcons, although it is present as a low intensity component of several displays. Rarely is the deep bowing, typical of large falcons, seen in Merlin displays. The Nest Ledge displays typical of both sexes of large falcons (which include much bowing) may be absent in the Merlin, being replaced by the very different male nest display, possibly as a result of the spacial limitations imposed by the stick nests typically used by Merlins in North America. Nest displays in ground nesting populations of Merlins may be different. Although we did not describe it as a separate display, scraping movements similar to those of cliffnesting falcons were made by our captive pair as evidenced by a well-developed nest scrape on a gravel ledge their first year (1981). Cramp and Simmons (1980) describe a Female Nest Display similar to the motions of settling on eggs, and we observed both sexes of wild pairs repeatedly visiting potential nests and could hear Tic-Tic vocalizations. Scraping on the stick nest cup may well be occurring at these times or possibly mild forms of the Nest Ledge Displays typical of large falcons.

Fanning or flashing the tail appears to be much more common in the Merlin than large falcons. It is often seen as a component of male displays and is typical of Copulation Solicitation of the female where the tail is kept fanned until actual mounting by the male. The sharply contrasting tail of the Merlin makes this a potentially strong visual stimulus. Merlin courtship behavior is decidedly more complex than that of the American Kestrel (F. sparverius), although the displays which are common to both species are similar. Two distinct aerial displays have been described for the kestrel, the Flutter Glide and the Dive display (Willoughby and Cade 1964). The Flutter Glide is performed by kestrels in much the same manner as Flutter Flying in Merlins. In the kestrel this type of flight is performed mainly by the female, while in Merlins it is more commonly performed by males. The kestrels' Dive Display is similar to the Undulating Flight Display of the peregrine and Gyrfalcon as described by Nelson (1977) and Cramp and Simmons (1980). We have not observed it in the Merlin although it is somewhat similar to Power Diving. The overall behavioral repertoire and intensity of displays of the Merlin is markedly more similar to the large falcons than to the kestrel.

Our lack of observations of overt intraspecific aggression directed toward non-resident birds was somewhat surprising as most falcons are thought of as being highly aggressive and territorial (Wrege and Cade 1977; Nelson 1977; Cade 1982). We have observed only 2 cases where actual physical contact between the resident bird (both males) and nonresident birds (also males) was made and both of these occurred in the fall. Only one case of overt aggression was observed during the courtship period when an adult male swooped on another male from a great height near a territorial boundary. The attacked bird screamed and was visibly upset, but no further interaction ensued. Nonresident birds (both adult and immature) were regularly seen on established nesting territories. Interaction ranged from completely ignoring the intruder to a variety of territorial displays, including Power Flying and Diving, Rocking Glide and Slow Landing Displays by the resident male. Earlier in courtship, before nest site selection and final establishment of territorial boundaries, group displays by several birds are not uncommon. Once such group display involved 4 adult males and at least 1 female (W.J.P. Thompson, pers. comm). Although it is often difficult to keep track of individual birds when several are present, we feel that copulation attempts (some successful) by non-resident males may occur relatively frequently.

Given the lack of intraspecific aggression directed towards non-resident birds by a territorial pair, it is somewhat surprising that the female of a pair is sometimes so aggressive towards her mate. At least in captivity, high proportions of females regularly attack their mates and often succeed in killing them. This appears to be much more frequent among Merlins than larger falcons. Similarly

interspecific aggression directed towards other raptors, crows, etc., is often intense and is carried out by both sexes.

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Department of Veterinary Anatomy, Western College of Veterinary Anatomy, University of Saskatchewan, Saskatoon, Saskatchewan, S7N OWO CANADA.